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THE PROTEIN OF THE SALVARY GLAND SECRETION IN DROSOPHILA

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At the beginning of the prepupal stage, the salivary gland of Drosophila becomes enormously inflated. This inflation is due to the appearance of a large amount of material in the lumen of the gland. Prior to the prepupal stage this material is in the cytoplasm of the gland cells but not in the lumen of the gland. It is undoubtedly the secretion released from the cells into the lumen soon after the larval stage terminates. The origin and movements of this material will be described in detail elsewhere.

If an inflated gland is isolated from the prepupa and its tissue is broken in water, the secretion flows out, and unless the water is distinctly acid it dissolves quickly, forming a viscous solution. If, on the other hand, an inflated gland isolated from a prepupa is placed in 95% alcohol, the secretion immediately hardens and becomes opaque while the tissue remains transparent. The secretion can be easily isolated in this condition by removing the tissue with needles under the dissecting microscope. The isolated secretion retains the same solubility in water as before alcohol treatment provided it is not kept too long in alcohol. If an isolated secretion is transferred to absolute alcohol, it immediately becomes brittle and loses its solubility in water except at high pH's. In its native state, i.e., before alcohol treatment, most of this material does not dissolve in common lipid solvents.

By separating the inflated glands from about 800 prepupae of *Drosophila melanogaster* in isotonic saline and isolating the secretions as completely as possible from the tissues in 95% alcohol, about 1600 pieces of secretion were collected. These were transferred to ether as soon as isolated from the tissues and exhaustively extracted, and the residue was thoroughly dried. From the weight of 600 pieces of the residue, the average weight of one piece of secretion was found to be approximately 4 μg. The ether-soluble

fraction of the secretion was found to be very small in proportion to the residue. Its chemical nature will be described elsewhere and only that of the residue will be reported here.

The residue is insoluble in all common organic solvents and even in dilute or concentrated mineral acids unless heated, but it dissolves readily in weak or strong alkali solutions without heating. A sample of residue was dissolved in dilute NaOH solution and the solution was neutralized with HCl and tested for various color reactions with the following results: positive for ninhydrin and biuret reactions; slightly positive for Molisch reaction; and negative for Millon's, Hopkins-Cole and xanthoproteic reactions. These results suggested that the substance is a protein containing an unusually small amount, if any, of aromatic amino acids. The ultra-violet absorption spectra showed no selective absorption between 210 μ and 310 μ. The absence of selective absorption at about 290 μ agrees with the negative color reactions for aromatic amino acids. The absence of selective absorption at 260 μ indicates absence of nucleic acids in the residue. These tests were repeated with several samples with consistently the same results. The residue is, therefore, not significantly contaminated with the gland tissue, for otherwise the nucleic acid would be detected. In fact, microscopic examinations revealed that the number of cells present in the residue was so extremely small that they can be entirely neglected. It may be added that the dissolved residue is precipitated by phosphotungstic acid but not by trichloroacetic acid.

The nitrogen content of the substance was found by micro-Kjeldahl analysis to be 10.8%. This figure was obtained from one sample of 4.8 mg. and it is unusually low for a protein. When samples of the residue were hydrolyzed with 10% HCl for 24 hours with constant boiling of the acid and when the acid was evaporated on a steam bath, a substantial amount of crystalline inorganic salt was found in the dry residue. Although the proportion of the salt in the samples was not determined, it seems that the unusually low figure for the N content found in the above analysis can well be accounted for by the presence of the inorganic salt, and a large amount of glutamic acid and some glucosamine, both of which have low nitrogen content (see below).

As a preliminary to the two-dimensional chromatogram analysis, three samples of small quantities of the residue were hydrolyzed with 10% HCl for 24 hours with constant boiling of the acid and the hydrolyzates were analyzed on filter paper strips, one with collidine and two with phenol as the solvent. For the principle and technique of the partition chromatogram method of protein analysis, the reader is referred to Consden, Gordon and Martin (1944)[1] and to Dent (1946)[2]. In one of the phenol strips an intensely colored band was present at $Rf = 0.21$. In the control strip in which glutamic acid was used, the Rf of the band was 0.20. In the other phenol strip a strongly colored band was also present at about the same

position. In the collidine strip also an intensely colored band was present at $Rf = 0.12$. In the control strip in which glutamic acid alone was used, the Rf of the band was 0.15. These bands in the experimental and control strips are sufficiently close to each other to indicate that the band in the experimental strip represents glutamic acid. Less intensely colored bands were found at various other positions on all three strips.

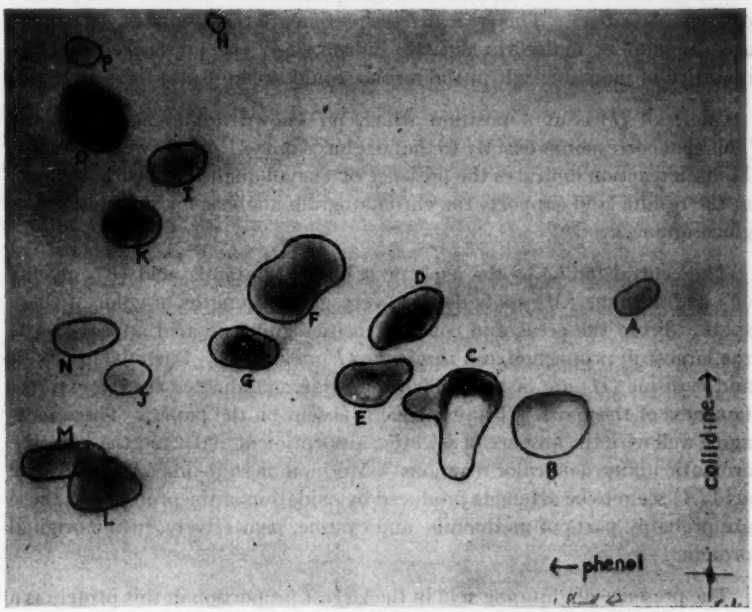

FIGURE 1

The result of a two-dimensional chromatogram analysis of the acid hydrolyzate of the protein in the secretion of the salivary gland in Drosophila is shown. Each circle represents one amino acid or an oxidation product of an amino acid. The hydrolyzate was put at the position of the cross at the lower right and phenol and collidine were run in the respective directions indicated by the arrows. *A*, cysteic acid; *B*, aspartic acid; *C*, glutamic acid; *D*, serine; *E*, glycine; *F*, threonine; *G*, alanine; *H*, tyrosine; *I*, glucosamine; *J*, methionine sulfoxide; *K*, valine; *L*, lysine; *M*, arginine; *N*, proline; *O*, leucine; *P*, phenylalanine.

Since most of the bands on the strips represented mixtures of two or more amino acids, a two-dimensional analysis was made to separate all the amino acids contained in the residue in order to identify them individually. Eight hundred μg. of the residue was taken for this purpose. This is about ten times as much as the amount required for an adequate analysis of an

ordinary protein by the chromatogram method. The residue was hydrolyzed with 10% HCl for 24 hours in a sealed glass tube placed in boiling water and the hydrolyzate was analyzed on a square filter paper with phenol and collidine as solvents. The result is shown in figure 1. Sixteen ninhydrin-positive spots are recognized, fifteen of which are identified as amino acids. The color of these spots is, on the original paper, only about half as intense as would be expected if the sample consisted entirely of a protein of usual N content. This indicates the presence in the residue of a considerable amount of ninhydrin-negative substance. The presence of a large quantity of inorganic salt in the residue could account also for this result.

One spot (*I*) is at a position which no known amino acid occupies. This spot corresponds exactly to that of glucosamine. A very weak, positive Molisch reaction indicates the presence of a small quantity of carbohydrate in the residue and supports the chromatogram analysis for the presence of glucosamine.

The central fading of the aspartic acid (*B*), glutamic acid (*C*), glycine (*E*) and arginine (*M*) spots denotes very great strengths of color of these spots. From the areas and color intensities glutamic acid appears to be the largest in proportion and threonine (*F*) next to it. Phenylalanine (*P*) and tyrosine (*H*) are of negligible proportion as indicated by the extreme faintness of the spots. Tryptophane is absent on the paper. These facts agree well with the absence of selective absorption at 290 μ and the negative aromatic amino acid color reactions. Methionine sulfoxide (*J*) and cysteic acid (*A*) seem to be artefacts produced by oxidation of the protein and these are probably parts of methionine and cystine, respectively, in the original protein.

The presence of glutamic acid in the largest proportion in this protein is a noteworthy characteristic, but not unusual as a number of proteins are known to contain a disproportionately large quantity of this amino acid. The unique feature, however, is the unusually large proportion of threonine (*F*) and serine (*D*). Dr. Dent informs me that he knows of no other protein so far analyzed by the chromatogram method which shows such an intensely colored and broad spot of threonine in relation to the other spots. Although an accurate quantitative determination is not possible, the fact that this spot is so unusually out of proportion indicates an extraordinarily high content of threonine in the protein of the residue. The serine spot is likewise unusually high in intensity in proportion to the other spots, indicating also an extraordinarily large content of this amino acid in the protein.

As pointed out already, this protein together with the ether-soluble substance is secreted into the lumen of the gland as soon as the animal begins to pupate. The secretion remains in the lumen for a short time and disap-

pears. Where it goes and what it is used for is now being investigated. Although no evidence has yet been obtained, the fact that it disappears from the gland at an early pupal stage suggests a possibility that it either enters into the formation of a part of the pupal body or participates in the chemical processes of histogenesis. One possible function it may have would be to provide through digestion a very large amount of glutamine. Glutamine readily enters into transamination reactions and its presence thus would provide an ample source of a variety of amino acids which must be required for the rapid rate of protein synthesis occurring at this stage of development. Similarly, serine which is present in an unusually large proportion in the secretion protein may, after being freed from the protein, become an abundant source of precursors of other amino acids such as glycine and cystine (Stetten, 1942).[3] As to threonine, which is contained also in an extraordinarily large amount in this protein, its possible use in histogenesis cannot be surmised, since only relatively little is known concerning the metabolism of this amino acid.

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[1] Consden, R., Gordon, A. H., and Martin, A. J. P., *Biochem. J.*, **38**, 224 (1944).
[2] Dent, C. E., *The Lancet*, Nov. 2, 1946.
[3] Stetten, A., *J. Biol. Chem.*, **144**, 501 (1942).

LINKAGE STUDIES OF THE RAT. IX. CATARACT

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Cataract is a dominant character discovered in an albino strain of rats by Smith and Barrantine, and described by them in the *Journal of Heredity*, **34**, 8–10, 1943. A stock of cataractous individuals, 3 females and 2 males, was kindly supplied to us for linkage studies in September, 1943.

No indications have been found of linkage between the gene for cataract and any other gene of the rat. The tests made and their results are summarized in table 1. The progress of the tests has been slow because the cataract is recognizable only in individuals which have unpigmented eyes albinos or pink-eyed yellows. Colored individuals must be subjected to

a breeding test in order to ascertain whether or not they are carriers of the gene for cataract.

The test procedure is as follows. A cross is made between a cataractous individual and an individual carrying the other gene to be tested, as for example, Cataract × Curly. An F_1 individual will carry *Ca* and *Cu* in the repulsion relationship.

Such an F_1 animal, if crossed to normal albinos, will produce four classes of offspring, of which the first and fourth will be crossover combinations, *Ca Cu*, *Ca*, *Cu*, and 0 (neither *Ca* nor *Cu*). If the sum of the crossover classes is significantly less than that of the other two classes, linkage will be indicated. In no cross made has such an indication been found. See table 1.

We conclude that the gene for cataract does not lie in any of the four known linkage systems, nor in chromosomes tagged by the genes, Cu_2, *j*, *d*, *A* and *h*. This indicates that it will serve as marker of a tenth chromosome.

TABLE 1

TESTS FOR LINKAGE BETWEEN THE DOMINANT GENE CATARACT (*Ca*) AND OTHER GENES OF THE RAT. KNOWN LINKAGE SYSTEMS INVOLVED IN THE TESTS ARE INDICATED BY ROMAN NUMERALS. FREQUENCIES OF CROSSOVER CLASSES ARE SHOWN IN ITALIC NUMERALS

	GENES	PROGENY CLASSES: REPULSION	PROGENY CLASSES: COUPLING	TOTAL CROSSOVERS	TOTAL NON-CROSSOVERS	GRAND TOTAL	DEV./P.E.
I	*Ca* × *p*	*Cap Ca* *99* 109		99	109	208	5.0/4.8
II	*Ca* × *Cu*	*CaCu Ca Cu* 0* *12* 20 28 *34*	*CaCu Ca Cu* 0 19 *21 27* 28	94	95	189	0.5/4.6
III	*Ca* × *k*	*Cak Ca k* 0 *7* 5 2 *1*		8	7	15	0.5/1.3
IV	*Ca* × *hr*	*Cahr Ca* *32* 26		32	26	58	3.0/2.5
IV	*Ca* × *wo*	*Cawo wo* *6* 6		6	6	12	0/1.1
	Ca × Cu_2	*CaCu*$_2$ *Ca* Cu_2 0 *111* 135 160 *158*		269	295	564	13.0/8.0
	Ca × *j*	*Caj Ca j* 0 *13* 5 6 *8*	*Caj Ca j* 0 17 *16 17* 20	54	48	102	3.0/3.4
	Ca × *d*	*Cad Ca d* 0 *11* 17 6 *6*		17	23	40	3.0/2.1
	Ca × *A*	*CaA Ca A* 0 *13* 4 11 *3*	*CaA Ca A* 0 14 *10 11* 12	37	41	78	2.0/2.9
	Ca × *h*	*Cah Ca h* 0 *1* 2 3 *6*	*Cah Ca h* 0 3 *3 11* 5	21	13	34	4.0/1.9

* Showing neither gene.

THE SUPPRESSION OF CROSSING OVER IN INVERSION HETEROZYGOTES OF DROSOPHILA PSEUDOOBSCURA

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Observations and experiments on natural and artificial populations of *Drosophila pseudoobscura* have shown that within a given population flies of which the third chromosomes differ in gene arrangement (inversion heterozygotes) often possess higher adaptive values than those of which the homologous pair has the same arrangement in both chromosomes (inversion homozygotes).[1, 2] In many localities the inversion heterozygotes outnumber the homozygotes. The welfare of the populations of these localities, therefore, seems to depend upon the maintenance of a high adaptive level in the inversion heterozygotes relative to the homozygotes. In other localities, however, the populations consist mainly or entirely of inversion homozygotes. In these the adaptive level of the homozygotes must be at least tolerably high.

In theory, two genetic mechanisms could bring about adaptive differences between and among the inversion homozygotes and heterozygotes. First, the action of genes in development may be altered simply by differences in their order within the chromosome (position effect). Second, chromosomes with different gene arrangements may be essentially alike but may carry different complexes of genes which make their possessors physiologically and adaptively different. At the same time they might be co-adapted in such a way as to produce the higher adaptive level of the inversion heterozygotes. Of these two mechanisms the first, position effect, may or may not play a rôle in the evolution of the third-chromosome inversions of this fly. However this may be, the second is both effective and important. For if the superior adaptiveness of inversion heterozygotes were due to position effect alone, then each arrangement would be expected to have the same relative superiority regardless of the geographic origin of the chromosomes concerned. This is not the case. The evidence shows that inversion heterozygotes are adaptively superior to the corresponding homozygotes only if the chromosome pair has been drawn from the same or neighboring localities. They are no longer superior when each member of the pair is drawn from distant populations (as for example, from southern California and the central Sierra Nevada). The gene contents of the chromosomes from these populations are not co-adapted to each other in such a way as to produce adaptively superior heterozygotes when combined.[3]

The biological function of inversions in the natural populations of

Drosophila and their principal rôle in the evolution of these insects might be conceived to be the suppression of crossing over between gene complexes which have reached an adaptive equilibrium. Crossing over would destroy these complexes and would result in gene combinations of different adaptive values, but would be prevented by the binding effect of the inversions. Any inversion which is intrinsically neutral, that is, which produces no position effects, would accordingly spread through a population provided that it would guard from disintegration a gene complex well adapted to the habitat concerned. This would be particularly important where the highest adaptive values are found in heterozygotes. The degree to which such gene complexes are maintained by the binding effect of inversions would accordingly depend upon the degree to which crossing over is suppressed. The present study was designed to secure this information.

TABLE 1

RECOMBINATION OBSERVED IN THE CROSS *or Sc pr cv* ♀ × *or Sc pr cv* ♂

		WILD			
		STANDARD	ARROWHEAD	CHIRICAHUA	TREE LINE
0	wild type	2035	4473	3748	2708
	or pr cv	769	1251	873	558
1	*or*	1781	175	14	3
	pr cv	738	62	1	2
2	*or pr*	357	2	..	..
	cv	425	7	..	..
1,2	*or cv*	260	..	..	..
	pr	311	4	..	..
Total		6676	5974	4636	3271

Three wild strains of *Drosophila pseudoobscura* carrying Standard, Arrowhead and Chiricahua gene arrangements, respectively, and a strain carrying the Tree Line arrangement were employed. The former were originally collected at Piñon Flat, San Jacinto Mountains, California, the latter was collected at Mather, California, in the Sierra Nevada. The inversion heterozygotes of both localities are known to be adaptively superior to the homozygotes. The third chromosomes bearing the gene arrangements designated have been described previously.[4] Flies of each strain were outcrossed to a strain homozygous for the third chromosome recessives *orange* (*or*), *purple* (*pr*), *crossveinless* (*cv*) and the dominant *Scute* (*Sc*). The *or Sc pr cv* chromosome is known to have the Standard arrangement. F_1 females resulting from this cross, were then testcrossed to *or Sc pr cv* males. The progeny counts of the testcrosses are summarized in table 1. The gene *Sc* was disregarded in the counts because its manifestation in heterozygous condition is variable in different strains.[5]

The observed percentages of recombinations are as follows:

INTERVAL	STANDARD	ARROWHEAD	CHIRICAHUA	TREE LINE
or-pr	46.3	4.0	0.3	0.15
pr-cv	20.3	0.2	0	0

Because the distance in the chromosome between the genes *or* and *pr* is so great that considerable double crossing over must take place in the flies with Standard chromosomes, another experiment was arranged. The four wild type strains were crossed to flies which carried a third chromosome with the recessives *or* and *pr* and the dominants *Blade* (*Bl*) and *Sc*. F_1 females showing *Bl* and *Sc* were selected from the progeny and testcrossed to homozygous *or pr* males. The progeny counts of this testcross are shown in table 2.

TABLE 2

RECOMBINATION OBSERVED IN THE CROSS *or Bl Sc pr* ♀ × *or pr* ♂

		WILD			
		STANDARD	ARROWHEAD	CHIRICAHUA	TREE LINE
0	wild type	1933	3555	7483	2218
0	*or Bl Sc pr*	1147	1954	3046	725
1	*or*	313	99	27	7
1	*Bl Sc pr*	220	54	21	..
2	*or Bl*	562	17	1	..
2	*Sc pr*	408	9	2	..
3	*or Bl Sc*	892	6	..	..
3	*pr*	922	11	..	..
1, 2	*Bl*	3	..	..	..
1, 2	*or Sc pr*	6	..	..	..
2, 3	*Bl Sc*	81	..	..	..
2, 3	*or pr*	88	1	2	..
2, 3	*Sc*	84	..	..	..
2, 3	*or Bl pr*	105	..	..	..
Total		6764	5706	10582	2950

The following percentages of recombination have been computed from the data in table 2.

INTERVAL	STANDARD	ARROWHEAD	CHIRICAHUA	TREE LINE
or-Bl	10.5	2.7	0.5	0.2
Bl-Sc	17.3	0.5	0.03	0
Sc-pr	32.1	0.3	0.02	0

The standard map distance obtained in our experiments between the loci furthest apart, *or* and *cv*, is 80.2 units, or slightly higher than the figure 68.4 units, obtained by Tan[6] from somewhat less extensive data. It may also be noted that Tan's experiments were conducted at 25°C., ours at ±18°C. The location in the cytologically visible chromosome of

the genes used in our experiments can be inferred from the chromosome map published by Tan.[7] As seen in the salivary gland cells, the third chromosome is a ribbon-like structure which for purposes of description has been subdivided into nineteen more or less equally long sections numbered 63 to 81, inclusively. The gene *or* lies in section 65 at a distance from the centromere of about one-tenth the length of the whole chromosomes. The centromere is in section 63. The gene *cv* lies somewhere in sections 79–81, close to the free end of the chromosome. The map distance of 80 units between *or* and *cv* therefore represents most of the genetic length of the third chromosome. Taking into account the fact that some double crossing-over has remained undetected, and also that between one-tenth and one-fifth of the cytological chromosome contains no known genetic markers, the linkage map of this chromosome is probably less than 100 units long.

The total frequency of recombination found in Standard/Arrowhead heterozygotes is about 4.0 per cent, in Standard/Chiricahua 0.5 per cent and in Standard/Tree Line only 0.2 per cent. Arrowhead differs from Standard by a single inversion which includes sections 70–76 or about one-third the length of the chromosome.[4] Tan[7] places the gene *Sc* within, and *pr* outside and distal to the Arrowhead inversion, but his data regarding *pr* are inconclusive. *Bl* and *or* certainly lie between the inversion and the centromere. In Standard/Arrowhead heterozygotes less than one-fiftieth of the recombination normally taking place in the *pr-cv* interval is permitted, and about one-fifteenth of recombination between *or* and *pr*, most of it in the *or-Bl* interval. In other words, an inversion exerts a relatively greater suppressive effect on recombination in the part of the chromosome which lies distal to it (between the inversion and the free end of the chromosome) than it does on recombination between the centromere and the inversion. This agrees with the data of Sturtevant[8] for *Drosophila melanogaster*.

The Chiricahua and Tree Line arrangements differ from the Standard each by a triple inversion which extends from about the middle of section 68 to section 79, inclusive, or about six-tenths of the length of the chromosome as seen in the salivary gland cells.[4] Our data show that recombination in Chiricahua/Standard and Tree Line/Standard is almost wholly suppressed in the whole of the third chromosome. The small amount still permitted, less than six-tenths per cent, is concentrated between the genes *or* and *Bl*, a negligible amount being found elsewhere. Particularly noteworthy is the fact that crossing-over is very strongly suppressed between the centromere and the inversions, the result, probably, of interference by the inversions with meiotic pairing.[9] No recombination whatsoever is detectable in the inverted part of the chromosome. (The three *or pr* flies recorded in table 2 among Standard/Chiricahua and

Standard/Tree Line heterozygotes are most likely the result of contamination; otherwise, they must represent triple crossovers, one between *or* and the inversion and a double to include the locus of *pr;* the individuals concerned were not tested further.)

The amount of crossing over within the inverted parts of the chromosome cannot be determined from our data, since single crossing-over in paracentric inversions does not result in detectable recombination.[10] However, single crossing-over in multiple inversions may result in deficiencies and duplications which produce unviable zygotes. The Standard/Tree Line heterozygotes, for example, have a long paired region which extends from section 68 to 74 (see Fig. 3 in Dobzhansky[4]). Crossing-over in this region would result in chromosomes which would act as lethals in zygotes. Whether such crossing over actually takes place is unknown; in neither case would viable chromosomes carrying gene recombinations normally borne in Standard and in Tree Line (or Chiricahua) appear. The possibility cannot be excluded that in inversion heterozygotes chiasmata may be localized in the immediate vicinity of the centromere, but crossing-over at the centromere would give no recombinations of the genes in Standard, Tree Line and Chiricahua chromosomes.

Summary.—Heterozygosis for inversions found in the third chromosome in natural populations of *Drosophila pseudoobscura* reduces the frequency of recombination of genes located in the chromosome to a small fraction of the normal value. Recombination is strongly prevented not only for genes within the inverted sections, but also for those which lie between the centromere and the inversion, and between the inversion and the free end of the chromosome. Inversion is therefore a powerful means of holding together gene combinations which confer upon their carriers superior adaptive properties.

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[2] Dobzhansky, Th., and Levene, H. Unpublished data.

[3] Unpublished data.

[4] Dobzhansky, Th., in Dobzhansky and Epling, Carnegie Inst. Washington, Publ. 554, 47–144 (1944).

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[7] Tan, C. C., *Z. Zellforsch. u. mikroscop. Anat.*, **26**, 439–461 (1937).

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THE RÔLE OF MUTATION AND OF SELECTION IN THE FREQUENCY OF MUTANTS AMONG MICROÖRGANISMS GROWN ON IRRADIATED SUBSTRATE

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The mutation rate in microörganisms is increased by irradiation or chemical treatment of the substrate.[1, 2] The problem of differentiating between the selection of spontaneous mutants and the induction of additional mutants is difficult, especially as the mutation rates are low and the growth rate of bacteria on treated substrate may be slower than normal. If selection is to explain the increase in frequency of mutants found in irradiated broth over that found in normal broth, it must increase the reproductive rate of mutants or inhibit it less than it inhibits the growth of normal cells. The increased number of mutants found in irradiated broth must be explained by induced mutation if selection is neutral or against the mutants.

Experimental.—The procedures for irradiating the medium with ultraviolet light and determining the drug resistant mutants are essentially those employed in our earlier reports.[1, 2] In addition to the stock strain of *Staphylococcus aureus* (F.D.A. #209) the first experiments reported here involved a penicillin resistant strain and a streptomycin resistant strain which arose as mutants when the stock strain was grown in irradiated broth. Identical inocula from 4-hour log phase cultures and also from 24-hour cultures (older cultures do not give consistent results) of each strain were planted in plain nutrient broth (control) and in irradiated nutrient broth. Immediately after inoculation and again after five hours, samples from each bottle were withdrawn for plating to determine the total count and the number of drug-resistant individuals in each population.

In table 1 are given the number of mutants per million organisms which are resistant to the indicated concentrations of the antibiotics, except for the figures in italics which show the total plate counts. The age of the inocula appeared to have little effect on the behavior of the organisms and the two portions of the table may be regarded as replicate experiments. Since these cultures produce a maximum of about 300 million cells per ml. under the conditions employed, it is evident that all cultures were still in the rapid growth phase at the 5-hour plating. The amount of radiation to which the broth was exposed was such that in no case did the culture growing in the irradiated broth fall behind the replicate growing in the control broth by as much as one division during the 5-hour growth period.

TABLE 1

EFFECT OF IRRADIATION OF THE BROTH ON THE GROWTH AND MUTATION RATE OF NORMAL AND DRUG-RESISTANT *S. aureus*

	24-HR. INOCULUM				4-HR. INOCULUM			
	CONTROL		IRRADIATED		CONTROL		IRRADIATED	
	0	5	0	5	0	5	0	5 HRS.
Normal Strain								
Total count, millions*	*2.4*	*75*	*1.8*	*52*	*0.86*	*65*	*1.1*	*47*
Penicillin, 0.07 u/ml.	13	19	17	344	7.0	4.6	9.3	40
Streptomycin, 3.0 u./ml.	65	41	79	310	48	23	46	185
Streptomycin, 6.0 u./ml.	42	12	36	123	10	1	2.8	40
Penicillin Resistant Strain								
Total count, millions*	*1.5*	*60*	*1.7*	*41*	*0.73*	*80*	*1.1*	*54*
Penicillin, 0.07 u./ml.	18T	999T	17T	850T	14.5T	1.8T	6T	14T
Streptomycin, 3.0 u./ml.	49	40	40	215	53	10	53	196
Streptomycin, 6.0 u./ml.	19	32	12	98	5.5	6.3	3.5	21
Streptomycin Resistant Strain								
Total count, millions*	*0.78*	*68*	*0.82*	*53*	*1.8*	*67*	*1.6*	*60*
Penicillin, 0.07 u./ml.	5.1	6.5	16	70	9.2	3.9	21	85
Streptomycin, 3.0 u./ml.	500T	280T	330T	226T	302T	78T	260T	180T
Streptomycin, 6.0 u./ml.	94T	66T	73T	12.8T	80	30	180	775

* Figures in italics are total count in millions determined by plating on nutrient agar. Other figures are the number of mutants (per million of the total count) which grew on the indicated antibiotic concentration. (T = thousand)

Yet during this period the proportion of mutants in the normal population grown in the irradiated broth increased many-fold.

It is clear that the penicillin resistant mutant resembles the normal strain in its rate of mutation to streptomycin resistance under the several test conditions. Likewise, the normal and streptomycin resistant strains have similar mutation rates to penicillin resistance. These rates, measured by rate of occurrence of organisms which grow at the indicated antibiotic concentrations, vary considerably but give a fairly consistent pattern. There is an increase in the number of resistant cells after growth on irradiated broth. However, when the changes in penicillin resistance in the penicillin resistant strain and of streptomycin resistance in the streptomycin

resistant strain under the several test conditions are compared, there is no consistent relation. In only a few instances did all the cells in the so-called resistant strains actually grow in the concentration of the antibiotic employed. Sometimes more appeared under control conditions, sometimes more from the irradiated broth. This is not in harmony with the idea that irradiated broth either conditions or selects for resistant organisms.

Selection could account for the increase in numbers of mutants in the irradiated broth only if the normal bacteria were slowed down in reproductive rate or killed, while the multiplication of the resistant mutants was speeded up or at least not retarded to the same extent. The number of times that the populations increased during the 5 hours was computed from the data on table 1. These figures for the total population and for those fractions which grew in the presence of 0.07 unit per ml. penicillin or 3 units per ml. streptomycin are recorded in table 2.

TABLE 2

INCREASE IN 5 HOURS OF THE TOTAL CELL COUNT AND OF THE MUTANTS EXPRESSED AS MULTIPLES OF THOSE PRESENT IN THE INOCULUM

	24-HR. INOCULUM			4-HR. INOCULUM		
	CONTROL	IRRADIATED	RATIO	CONTROL	IRRADIATED	RATIO
Normal Strain						
Total count*	31 (5.0)	28 (4.8)	0.9	76 (6.2)	43 (5.4)	0.6
Penicillin mutants	45 (5.5)	575 (9.2)	13	50 (5.7)	185 (7.6)	3.7
Streptomycin mutants (3.0)	20 (4.2)	110 (6.8)	5.5	36 (5.2)	175 (7.4)	5
Penicillin Resistant Strain						
Total count	40 (5.4)	24 (4.6)	0.6	110 (6.8)	49 (5.6)	0.4
Streptomycin mutants (3.0)	33 (5.1)	128 (7.0)	4	21 (4.4)	181 (7.5)	8.6
Streptomycin Resistant Strain						
Total count	87 (6.5)	65 (6.0)	0.7	37 (5.2)	37 (5.2)	1
Penicillin mutants	112 (6.8)	285 (8.2)	2.5	16 (4.0)	150 (7.2)	9.4

* Figures in parentheses give number of bacterial generations required to produce 5-hour population from inoculum.

Growth of the normal and the streptomycin resistant strains in irradiated broth was only slightly less than in control broth but the penicillin mutant was inhibited to a greater extent. Both the penicillin resistant mutant and the streptomycin resistant mutant were originally isolated from irradiated broth. If selection is to account for the increase in number of organisms resistant to antibiotics in irradiated broth, these mutants should have a positive selection value in irradiated broth. This is not the case. Therefore, selection fails to explain the increase in numbers of organisms resistant to antibiotics in the irradiated broth.

Table 2 shows the differential increase in resistant organisms in irradiated broth during the five-hour growth period. This is expressed both as multiplication of the original cells (normal and resistant) during that

TABLE 3

GROWTH AND MUTATIONS IN A MIXED CULTURE OF NORMAL AND MUTANT CELLS

	HRS.	CONTROL		IRRADIATED	
		MUTANTS PER MILLION	TOTAL IN MILLIONS	MUTANTS PER MILLION	TOTAL IN MILLIONS
		Normal Strain			
Penicillin, 0.07 u./ml.	0	20	1.3	16.7	0.7
	2	15.8	38	372	7.8
	5	9.8	102	316	38
Penicillin, 0.20 u./ml.	0	0	1.3	0	0.7
	2	0	38	8.6	7.8
	5	0.4	102	4.7	38
		Penicillin Resistant Strain			
Penicillin, 0.07 u./ml.	0	826T	0.58	1000T	0.5
	2	1000T	16.3	992T	1.4
	5	895T	67	1000T	13
Penicillin, 0.20 u./ml.	0	0	0.58	0	0.5
	2	0	16.3	203	1.4
	5	6.0	67	238	13
		Mixed Culture (0.9 Normal + 0.1 Resistant)			
Penicillin, 0.07 u./ml.	0	58T	1.7	48T	1.2
	2	41T	40	60T	5.3
	5	42T	96	58T	72

TABLE 4

GROWTH AND MUTATIONS IN A MIXED CULTURE OF NORMAL AND MUTANT CELLS

	HRS.	CONTROL		IRRADIATED	
		MUTANTS PER MILLION	TOTAL IN MILLIONS	MUTANTS PER MILLION	TOTAL IN MILLIONS
		Normal Strain			
Streptomycin, 3.0 u./ml.	0	25.3	0.8	29.8	0.8
	3	22.2	35	210	5.3
Streptomycin, 10 u./ml.	0	0	0.8	0	0.8
	3	0.6	35	5.1	5.3
		Streptomycin Resistant Strain			
Streptomycin, 3.0 u./ml.	0	925T	0.8	965T	0.6
	3	385T	19.4	429T	3.1
Streptomycin, 10 u./ml.	0	210	0.8	165	0.6
	3	66.8	19.4	935	3.1
		Mixed Culture (0.9 Normal + 0.1 Resistant)			
Streptomycin, 3.0 u./ml.	0	106T	1.2	124T	1.0
	3	56T	36.0	104T	7.2

period and as cell divisions necessary to give the net increase in numbers. The increase in number of resistant cells is of a consistently different order of magnitude from the differential increase in number of cells present in

irradiated and control media. Furthermore, the resistant mutants are similar to the normal strain in giving a differential increase in number of mutants resistant to the second antibiotic. These differences are expected if some substance in the irradiated broth causes an increase in the mutation rate. They are not in agreement with an explanation of the increase of resistant organisms based on selection.

Since it may be suggested that population dynamics in mixed cultures sometimes gives an unexpected advantage to one component, artificial mixtures of the normal and mutant organisms were prepared. The inoculum of the mixed cultures, which consisted of 9 times as many organisms from the normal strain as from the mutant strain, was planted in both irradiated and plain broth as were the requisite pure culture controls. At the time of inoculation and again 2 and 5 hours, or 3 hours later, the total count and the numbers of the mutants were determined (tables 3 and 4). It is evident that the mutants enjoyed no selective advantage in the irradiated broth. However, there was a definite and greater increase in the resistant strain of the mutants which grew in the higher concentration of antibiotics.

Another line of evidence is derived from experiments in which organisms were left in contact with the irradiated broth for varying periods of time and then washed and removed to normal broth to eliminate the possible selective action of inhibitory principles derived from the radiations. The procedure which included controls to test the effect of the washing and transferring process is described below and is outlined in the footnote of table 5.

Bottles of sterile unirradiated and irradiated nutrient broth (I A and II A) were inoculated with about 2×10^6 organisms per ml. from a log phase culture of *S. aureus*. After one-half hour a 10-ml. sample was withdrawn aseptically from each inoculated broth and placed in a sterile centrifuge tube; the bottles were incubated at 37°C. The samples were centrifuged and the sedimented organisms were washed with unirradiated broth and recentrifuged. The washed organisms were inoculated into bottles of unirradiated broth (I B and II B) from which samples were immediately withdrawn and plated in appropriate dilutions to determine the total numbers and the incidence of mutants. Further platings were made after 2- and 5-hour incubation at 37°C.

When the cultures in bottles I A and II A had been incubated $1^1/_2$ hours, another 10-ml. sample was withdrawn from each and the centrifuging and washing process performed as above. The washed organisms from the $1^1/_2$-hour cultures were inoculated into bottles of unirradiated broth (I C and II C) from which platings were made as before at 0, 2 and 5 hours after inoculation. In a like manner, a third sample was withdrawn from bottles I A and II A after they had been incubated 4 hours, but due to

TABLE 5

EFFECT OF THE TIME OF CONTACT WITH IRRADIATED BROTH ON SUBSEQUENT GROWTH AND MUTATIONS IN UNIRRADIATED BROTH

	HOURS AFTER INOCULATION								
	0			2			5		
BOTTLE	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*
	Experiment 1								
I A	2	6	32	..	...	...	65	88	177
II A	3	4	22	..	...	...	83	7	11
I B	0.6	16	48	6	65	158	83	46	57
II B	0.7	6	25	10	6	13	79	6	9
I C	0.8	69	159	24	50	115	63	103	374
II C	5.8	4	11	32	3	21	84	8	17
I D	0.8	100	186	12	82	262	63	35	145
II D	1.0	7	30	8	7	38	51	6	16
	Experiment 2								
I A	2	17	43	..	...	...	55	300	102
II A	2	12	26	..	...	...	96	1	8
I B	0.3	39	48	15	46	31	47	110	58
II B	0.4	12	31	19	8	6	55	2	8
I C	0.6	59	26	14	19	57	42	255	472
II C	2	15	20	33	1	6	87	4	14
I D	1	78	152	23	148	257	..	...	...
II D	2	2	11	26	6	14	..	...	...

a = total count per ml. in millions. *b* = mutants per million on 0.07 unit per ml. penicillin. *c* = mutants per million on 3 units per ml. streptomycin.

I A. Bottle of irradiated broth inoculated with log phase culture of *S. aureus*.

I B. Bottle of unirradiated broth inoculated with washed centrifuged cells which had grown in I A for $^1/_2$ hour.

I C. As I B but inoculum grown in I A for $1^1/_2$ hours.

I D. As I B but inoculum grown in I A for 4 hours.

II A, B, C, D. Same as the I series except that II A was unirradiated broth control.

growth of the culture the washed sedimented cells were diluted before inoculating into the bottles of unirradiated broth (I D and II D) so that the inoculum was about 10^6 cells per ml. The total count and the incidence of mutants in bottles I A and II A were determined immediately after inoculation and again after 5 hours' incubation.

The results of replicate experiments are given in table 5.

It should be emphasized that the value of these tests lies in the fact that bacteria were exposed first to irradiated broth and then transferred to normal broth. The table shows that the technique of centrifuging the bacteria did not modify the results appreciably, for the two controls are essentially alike. Further, the same increase in number of mutants present is apparent in bacteria grown in irradiated broth whether or not they were centrifuged and then grown in unirradiated broth. Also this table shows that if a "high" percentage of mutants were present when the bacteria were transferred into normal broth (i.e., after four hours in irradiated broth)

this frequency was retained as the bacteria grew in normal broth. Further, if the bacteria remained in the irradiated broth for only a short period ($1^1/_2$ hours or sometimes even $^1/_2$ hour), the number of mutants present after growth in normal media increased quite markedly. The irradiated media had affected the bacteria so that the mutation rate, measured in their descendants grown in normal broth, was markedly higher after several cell divisions. Demerec[3] observed a similar effect from direct irradiation. These results are in agreement with the hypothesis that some material in the media, when utilized in the cell, causes mutations which can show in the descendants of the cell. The increase in number of mutants after transfer into normal broth is not in agreement with an explanation based on selection for resistant organisms by irradiated broth.

TABLE 6

EFFECT OF IRRADIATED BROTH ON THE OCCURRENCE OF BIOCHEMICAL MUTANTS

	CONTROL			IRRADIATED		
STRAIN OF *S. aureus*	NO. TESTED	MUTANTS	NO. CELLS PER MUTANT	NO. TESTED	MUTANTS	NO. CELLS PER MUTANT
From mannitol + to −						
Rosenbach	4,000	0	..	349	1	349
	801	1	801	328	0	..
	3,976	2	1988	1,064	3	355
	....	..	..	3,477	9	386
	6,816	2	3408	10,974	15	731
	465	0	..	4,350	1	4350
Subtotal	16,058	5	3210	30,542	29	1073
Strain A	1,800	0	..	2,160	3	720
Strain B	4,600	1	4600	7,000	5	1400
Strain C	2,100	0	..	4,320	4	1080
Subtotal	8,500	1	8500	13,480	12	1123
TOTAL	24,558	6	4093	44,022	41	1074
From mannitol − to +						
	1,403	0		3,666	18	
	542	0		6,750	1	
	7,448	0		4,000	3	
	3,666	0		....	..	
	15,660	0		....	..	
TOTAL	28,719	0		14,416	22	655

The third series of experiments concern a different property of the organism, the ability to utilize mannitol. The normal strain of *S. aureus* used can ferment mannitol; it produces mutants which cannot. These mannitol negative organisms can in turn give rise to mannitol positive strains, presumably by reverse mutation. Table 6 shows that both the

direct and reverse mutation rate are increased by treatment with irradiated broth. The several different strains tested acted essentially alike. Grown in normal media, the combined mutation rate from mannitol + to − is one mutation in 4093; on irradiated media one in 1074; or roughly four times as great. No reverse mutation from − to + was discovered in 28,719 tested organisms grown on unirradiated broth, but 22 were found in 14,416 (1 in 655) among organisms grown in irradiated broth. The tables show the fluctuations in frequency of mutants in the several samples as would be expected from a mutation phenomenon. Although it was not proved that these − to + were reverse mutations, this theory is consistent with the situation in higher organisms. Whatever may be the truth of that matter, it is exceedingly difficult to explain how irradiated broth could select both for and against the ability to ferment mannitol.

Summary.—If selection is to explain the increased occurrence of mutants when *S. aureus* is grown in irradiated broth, the following conditions should be met: (1) Quantitative experiments should show that the mutants have a selective advantage over the normal strain under these conditions. This should be especially evident in a mixed culture. (2) When organisms are centrifuged from irradiated broth after a short exposure period and inoculated into unirradiated broth, the increase in the number of mutants should cease. (3) Both forward and reverse mutations should not be differentially increased by growth in irradiated broth. The results of our experiments do not fulfill any of these conditions. The results are in agreement with the hypothesis that mutations are induced by some factor in the irradiated broth.

[1] Stone, W. S., Wyss, O., and Haas, F., these PROCEEDINGS, **33**, 59–166 (1947).
[2] Wyss, O., Stone, W. S., and Clark, J. B., *J. Bact.*, **54**, 767–772 (1947).
[3] Demerec, M., these PROCEEDINGS, **32**, 36–46 (1946).

ON THE AVERAGE VALUE OF ARITHMETIC FUNCTIONS

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The purpose of this note is to introduce a new method of estimating sums of the form

$$S = \sum_{1 \leq n \leq N} f(g(n)), \tag{1}$$

where $f(n)$ is an arithmetic function such as the Euler totient function, $\phi(n)$, or the Dirichlet divisor function, $d(n)$, and $g(n)$ is either a polynomial

in n, a linear term of the form $ap_n + b$, where p_n is the nth prime, or an exponential term of the form $ak^n + b$.

We shall sketch the method in outline and then give the essential particulars for the sum

$$S = \sum_{1 \leq n \leq N} \sigma(P_k(n)), \tag{2}$$

where

$$\sigma(n) = \sum_{d|n} d, \tag{3}$$

and $P_k(n)$ is a polynomial of degree k with integer coefficients. A general investigation of results of this type will be presented subsequently.

The illustrious Indian mathematician, Ramanujan, was the first to appreciate the importance of the function

$$c_q(n) = \sum_{(p,\,q)=1} \exp(2\pi ipn/q), \qquad 1 \leq p \leq q, \tag{4}$$

in the analytic theory of numbers. He gave many interesting expansions involving these functions, of which the following are a sample:

$$\frac{\sigma(n)}{n} = \frac{\pi^2}{6} \sum_{q=1}^{\infty} c_q(n)/q^2 \tag{5}$$

$$d(n) = \sum_{q=1}^{\infty} c_q(n) \log q/q$$

The formulas seem to constitute an important link between the additive and multiplicative properties of numbers. There are several ways of deriving these striking formulas following methods of Hardy, Estermann, or Ramanujan himself. The author has derived another method which was used to state sufficient conditions for the expansion of a function in such a series. These results have been applied to estimation of the generalized Ingham sums of the form,[1]

$$\sum_{1 \leq n \leq N} f(n)f(n + k), \tag{6}$$

Returning to (1), we see that if

$$f(n) = \sum_{q=1}^{\infty} a_q c_q(n), \tag{7}$$

then

$$S = \sum_{1 \leq n \leq N} f(g(n)) = \sum_{q=1}^{\infty} a_q \left\{ \sum_{n=1}^{N} c_q(g(n)) \right\} \tag{8}$$

$$= \sum_{q=1}^{\infty} a_q \left\{ \sum_{(p,\,q)=1} \left\{ \sum_{n=1}^{N} e^{2\pi ipg(n)/q} \right\} \right\}$$

Sums of the form

$$E(N, g, q) = \sum_{n=1}^{N} \exp(2\pi i p g(n)/q) \tag{9}$$

have been the subject of considerable research in connection with Waring's problem. They are also of great intrinsic interest. The following result, due to Hua,[2] is fundamental.

LEMMA 1. *Let* $g(n) = \sum_{l=0}^{k} a_k x^k$, $(a_0, a_1, \ldots, a_k) = 1$. *Then*

$$\left| E(N, g, q) - \frac{N}{q} \sum_{n=1}^{q} \exp\left(\frac{2\pi i p g(n)}{q}\right) \right| = O(q^{1-1/k+\epsilon}), \tag{10}$$

where the constant implied by O is independent of N, p, and q, depending only on k and ϵ.

The estimate is most useful for $q \leq N$. Hence, the sum for $f(g(n))$ is broken into two parts, $(1, N)$, and $(N+1, \infty)$. The sum from $N+1$ to ∞ is estimated trivially, if $|a_q|$ is small enough as $q \to \infty$. For the case of $d(n)$ where the series is no longer absolutely convergent, difficulties arise.

We now use the above Lemma to prove

THEOREM. *Let* $g(n) = \sum_{l=0}^{k} a_l x^l$, $(a_0, a_1, \ldots, a_k) = 1$. *Then as* $N \to \infty$

$$\sum_{n=1}^{N} \sigma(g(n)) \sim \frac{a_k N^{k+1}}{k+1} \sum_{q=1}^{\infty} \frac{1}{q^3} \sum_{(p,q)=1} \left\{ \sum_{n=1}^{q} \exp(2\pi i p g(n)/q) \right\}. \tag{11}$$

The case where $(a_0, a_1, \ldots, a_k) > 1$ may be treated similarly, requiring only slight attention to details.

Proof: We treat $\sum_1 \sigma(g(n))/g(n)$ first and then use partial summation.

$$\frac{\sigma(g(n))}{g(n)} = \frac{\pi^2}{6} \sum_{q=1}^{N} \frac{c_q(g(n))}{q^2} + \frac{\pi^2}{6} \sum_{N+1}^{\infty} \frac{c_q(g(n))}{q^2} \tag{12}$$

$$= P(n) + R(n).$$

Let us estimate $R(n)$. It is known, elementarily, that

$$c_q(n) = \sum_{\delta|(q,n)} \delta \mu(n/\delta) \tag{13}$$

Hence

$$|c_q(n)| \leq \sum_{\delta|(q,n)} \delta = \sigma((q, n)) \leq (q, n) d((q, n)) \tag{14}$$

since

$$\sigma(n) = \sum_{\delta|n} \delta \leq n \sum_{\delta|n} 1 \leq n d(n). \tag{15}$$

Thus

$$|R| \leq \frac{\pi^2}{6} \sum_{N+1}^{\infty} (q, g(n))d((q, g(n))/q^2 \tag{16}$$

$$\leq \frac{\pi^2}{6} \sum_{\sigma|g(n)} \sigma d(\sigma) \sum_{(q,\, g(n)) = \sigma} {}^{1}/_{q^2},\ N+1 \leq q < \infty.$$

$$\leq \frac{\pi^2}{\sigma} \sum_{\sigma|g(n)} \frac{d(\sigma)}{\sigma} \left\{ \sum_{[N+1/\sigma]+2 \leq q < \infty} {}^{1}/_{q^2} \right\}$$

Considering separately the two cases $\sigma > \sqrt{N}$, $\sigma < \sqrt{N}$, we see that $|R|$ is less than

$$\frac{c_2 d^2(g(n))}{\sqrt{N}} = o(1), \tag{17}$$

since $d(n) = O(n^{\epsilon})$ for any $\epsilon > 0$. Thus it is clear that

$$\sum_{n=1}^{N} R(n) = o(N). \tag{18}$$

Using Hua's theorem, Lemma 1, in connection with $\sum_{n=1}^{N} P(n)$, and then summation by parts, we obtain the result stated in Theorem 1.

To obtain results for primes, we require estimates for trigonometric sums involving primes. For exponential terms, results concerning primitive roots are needed.

[1] Bellman, R., "On Ingham Sums and Ramanujan Expansions," unpublished.

[2] Hua, L. K., "On an Exponential Sum," *J. Chin. Math. Soc.*, **2**, 301–312 (1940).

AN INVERSION AND REPRESENTATION THEORY FOR CONVOLUTION TRANSFORMS WITH TOTALLY POSITIVE KERNELS

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Let b, $\{a_i\}_1^{\infty}$ be real constants subject to the sole restriction that $\sum_1^{\infty} (1/a_k)^2 < \infty$. It is easily verified that the formula,

$$G(t) = \frac{1}{2\pi i} \int_{-i\infty}^{i\infty} \frac{e^{st}}{e^{bs} \prod_1^{\infty} \left(1 - \frac{s}{a_k}\right) e^{s/a_k}}\, ds, \tag{1}$$

defines $G(t)$ as a real-valued function of t for $(-\infty < t < \infty)$, and that $G(t) \in C^\infty$. The problem of inverting the convolution transform with $G(t)$ as kernel,

$$f(x) = \int_{-\infty}^{\infty} G(x - t)\phi(t)dt, \tag{2}$$

has been considered by D. V. Widder.[1] In a note[2] in these PROCEEDINGS he announced that if $\phi(t) \in L$ and if x is a point of continuity of $\phi(t)$ then

$$\lim_{n \to \infty} P_n(D)f(x) = \phi(x), \tag{3}$$

where

$$P_n(D) = e^{(b-b_n)D} \prod_{k=1}^{n} \left(1 - \frac{D}{a_k}\right) e^{D/a_k},$$

the b_n being any real constants such that $\lim_{n\to\infty} b_n = 0$. Here the symbol D represents the operation of differentiation and $e^{D/a}$ the operation of translation through a distance $1/a$. In preparing the detailed proof of this result the authors discovered it could be much improved. It is the purpose of the present note to state these more general results. We have succeeded in removing all restrictions from $\phi(t)$ except those required to make the integral (2) converge. We have also been able to treat the Stieltjes case,

$$f(x) = \int_{-\infty}^{\infty} G(x - t)e^{ct}d\alpha(t), \tag{4}$$

where c is an arbitrary real constant, which is inverted, as was to be expected, by

$$\lim_{n\to\infty} \int_{x_1}^{x_2} e^{-cx}P_n(D)f(x)dx = \alpha(x_2) - \alpha(x_1). \tag{5}$$

I. J. Schoenberg[3] has studied the functions $G(t)$ in considerable detail, and some few of our results, although obtained by different methods, overlap with his. When this is the case the priority is his. The functions $G(t)$ defined in (1) are examples of what he has called "totally positive" functions. They do not constitute all such functions, but they virtually do so, and we have therefore borrowed his suggestive terminology.

A kernel $G(t)$ belongs to Class I if there are both positive and negative a_k's; $G(t)$ belongs to Class II if there are only positive a_k's and if $\sum_1^\infty (1/a_k) = \infty$; $G(t)$ belongs to Class III if there are only positive a_k's and if $\sum_1^\infty (1/a_k) < \infty$. Either $G(t)$ or $G(-t)$ belongs to one of these classes.

We shall briefly indicate the new properties of $G(t)$ which we have

established. Theorem 1 may be obtained as a special case of more general results due to Schoenberg.

THEOREM 1. *If $G(t)$ is defined as in equation (1), then $G(t)$ is a frequency function with mean b and variance $\sum_1^\infty (1/a_k)^2$; moreover, $G(t)$ is bell shaped, i.e., $(d/dt)^n G(t)$ has precisely n changes of sign.*

THEOREM 2. *If $G_1(t)$ and $G_2(t)$ are defined as in equation (1) with constants b, $\{a_i\}_1^\infty$ and c, $\{d_i\}_1^\infty$ respectively, and if the $\{d_i\}_1^\infty$ are a subset of the $\{a_i\}_1^\infty$, then $G_1(t) - G_2(t)$ has at most two changes of sign.*

THEOREM 3. *If $G(t)$ is defined by equation (1) and if $G(t) \epsilon$ Class II then for $L = L(t)$ defined as a function of t by the equation,*

$$t = \sum_1^\infty \frac{L}{a_k(a_k + L)},$$

we have for all t sufficiently large, $t > T$,

$$-\frac{d}{dt} \log G(t) = L(t + b + o(1)),$$

where $o(1)$ represents a function of t which approaches zero as t becomes positively infinite.

Using these theorems and other results familiar in specific cases from the theory of the Laplace[4] and Stieltjes[5] transforms we have been able to prove

THEOREM 4. *If $G(t) \epsilon$ Class I, then if the transform (4) converges for any one value of x it converges for all values of x. Moreover, if x_1 and x_2 are points of continuity of $\alpha(t)$, then the inversion formula (5) is valid. If $c \geq \operatorname{Min}_{a_k > 0} [a_k]$, then $\alpha(+\infty)$ exists and x_2 may be taken as $+\infty$. If $c \leqslant \operatorname{Max}_{a_k < 0} [a_k]$, then $\alpha(-\infty)$ exists and x_1 may be taken as $-\infty$.*

THEOREM 5. *If $G(t) \epsilon$ Class II, then if the transform (4) converges for any one value of x, it converges for all larger values of x so that its region of convergence is of the form $\gamma_c < x < \infty$. [The transform may or may not converge at the abscissa of convergence γ_c.] Moreover, if x_1 and x_2 are points of continuity of $\alpha(t)$, then the inversion formula (5) is valid. If $c \geqslant Min\ [a_k]$, $k = 1, 2, \ldots$, then $\alpha(+\infty)$ exists and x_2 may be taken as $+\infty$.*

THEOREM 6. *If $G(t) \epsilon$ Class III, if $\alpha(t)$ is of bounded variation in every closed finite subinterval of $T < t < \infty$, and if the transform (4) converges for some one value of $x > T + b + \sum_1^\infty (1/a_k)$, then it converges for all such x. Moreover, if x_1 and x_2 are points of continuity of $\alpha(t)$, then the inversion formula (5) is valid. If $c \geqslant Min\ [a_k]$, $k = 1, 2, \ldots$, then $\alpha(+\infty)$ exists and x_2 may be taken as $+\infty$.*

Analogous theorems may be stated for the convolution transform (2), which is inverted by the operator (3) for every point of continuity x of ϕ.

We may further improve these results. Let us list some conditions on the a_k's and b_n's.

$$A. \quad \sum_{n+1}^{\infty} |a_k|^{-3} = o\left[\sum_{n+1}^{\infty} a_k^{-2}\right]^{3/2},$$

$$B. \quad b_n = o\left[\sum_{n+1}^{\infty} a_k^{-2}\right]^{1/2},$$

$$C. \quad b_n = O\left[\sum_{n+1}^{\infty} a_k^{-2}\right]^{1/2}.$$

If $\alpha(t)$ is supposed to be normalized, $\alpha(t) = 2^{-1}[\alpha(t+) + \alpha(t-)]$, and if conditions A and B are satisfied, then (5) holds even for points of discontinuity. If condition C is satisfied, then (3) holds for all t in the Lebesgue set of $\phi(t)$ and hence almost everywhere.

These results include as special cases, and in a few instances go beyond, the results obtained for the Laplace and Stieltjes transforms, their iterates,[6, 7] the Meijer transform,[8] etc. They are substantially best possible results.

The authors have further constructed a comprehensive representation theory. Such theories have been constructed for the Laplace and Stieltjes transforms by D. V. Widder,[4, 5] for the iterated Stieltjes transform by R. P. Boas, Jr., and D. V. Widder[9] and for the third iterate of the Laplace kernel by E. J. Akutowicz.[10] Dr. Boas[8] has further announced but not published a similar theory associated with the Meijer transform. The present theory includes all these results as special cases. Since the statements of the theorems are rather long, and since they can be readily surmised by anyone familiar with the foregoing particular theories, we shall state only one typical result.

THEOREM 7. *If $G(t) \in$ Class II then the conditions*

1. $f(x) \in C^{\infty} \quad (\gamma_c < x < \infty)$,
2. $f(x) = o\ (e^{\alpha_2 x}) \quad (x \to \infty)$,

where $\alpha_2 = Min \ [a_k]$, $k = 1, 2, \ldots$,

3. $P_n(D)f(x) \geqslant o \quad (\gamma_c - b + b_n - \sum_{1}^{n} 1/a_k < x < \infty) n = 1, 2, \ldots$

are necessary and sufficient that

$$f(x) = \int_{-\infty}^{\infty} G(x - t)d\alpha(t),$$

with $\alpha(t)$ non-decreasing and with abscissa of convergence less than or equal to γ_c.

[1] Widder, D. V., *Duke Math. J.*, **14**, 217–251 (1947).

[2] Widder, D. V., PROC. NAT. ACAD. SCI., **33**, 295–297 (1947).

[3] Schoenberg, I. J., *Ibid.*, **33**, 11–17 (1947).
[4] Widder, D. V., *Trans. Am. Math. Soc.*, **36**, 107–200 (1934).
[5] Widder, D. V., *Ibid.*, **43**, 7–60 (1938).
[6] Pollard, H., *Duke Math. J.*, **14**, 129–142 (1947).
[7] Pollard, H., *Ibid.*, **14**, 659–675 (1947).
[8] Boas, R. P., Jr., PROC. NAT. ACAD. SCI., **28**, 21–24 (1942).
[9] Boas, R. P., Jr., and Widder, D. V., *Trans. Am. Math. Soc.*, **45**, 1–72 (1939).
[10] Akutowicz, E. J., "The Third Iterate of the Laplace Transform," Thesis, Harvard (1947).

THE LAPLACE TRANSFORM FOR LOCALLY COMPACT ABELIAN GROUPS

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Introduction.—As has been shown by A. Weil[1] and others the classical theory of the Fourier transform for functions defined on the real line has a natural generalization to a theory of a transform taking functions defined on a locally compact Abelian group G into functions defined on the character group $\hat{G}$ of G. This theory includes as special cases the theory of n-tuple Fourier series and the theory of n dimensional Fourier transforms. It is based upon the very simple idea of replacing the function $\exp(ity)$ which occurs in the classical one-dimensional Fourier transform by the character function (t, y) whose value for each t in G and each y in $\hat{G}$ is the value at t of the character y; and thus defining the Fourier transform of a suitably restricted $f(t)$ as $\int f(t)(t, y)dt$ where integration is with respect to the Haar measure in G.

It is the purpose of the present note to describe how this idea may be further exploited so as to generalize the Laplace transform and the Laurent series in an analogous fashion and thus to connect certain aspects of complex variable analysis with the theory of topological groups in the same way that this is done for real variable analysis by the generalized Fourier transform. It is hoped that ultimately such considerations will throw light on the theory of functions of several complex variables.

At the present time we are in a position only to describe the basic notions and state a few preliminary results. We expect to publish later in another journal a paper giving detailed proofs of the theorems stated here as well as those of others which we hope to obtain.

Real Characters, Linear Functionals and One-Parameter Subgroups.—We shall call a continuous complex valued function z, defined on the

locally compact Abelian group G, a generalized character if $z(t_1t_2) = z(t_1)z(t_2)$ for all t_1 and t_2 in G. It is evident that every generalized character has a unique representation as the product of two generalized characters, one of which takes its values on the positive real axis and the other on the unit circle. The generalized characters of the latter sort are clearly identical with the characters of the Pontrjagin-van Kampen duality theory and will be referred to as ordinary characters. Generalized characters of the former sort will be called real characters. If r is a real character then the function x obtained by setting $x(t) = \log(r(t))$ has the property that $x(t_1t_2) = x(t_1) + x(t_2)$ for all t_1, t_2 in G. A continuous real valued function with this property will be called a linear functional. Clearly the above-described mapping sets up a one-to-one correspondence between the real characters and the linear functionals on G. Now let x be any linear functional on G. For each real number u the function taking t in G into the complex number $\exp(iux(t))$ is clearly an ordinary character $y(u)$. Moreover $y(u_1 + u_2) = y(u_1)y(u_2)$ and y is a continuous function of u. Thus $y(u)$ is a continuous homomorphism of the additive group of the real line into $\hat{G}$. Such a homomorphism is called a one-parameter subgroup of $\hat{G}$. It may be proved without great difficulty that every one-parameter subgroup of $\hat{G}$ may be obtained from a linear functional in the manner just described and that there is thus obtained a one-to-one correspondence between linear functionals on G and one-parameter subgroups in $\hat{G}$. We shall find it convenient to use the same symbol to denote a linear functional and the corresponding one-parameter subgroup and to call the compound object so denoted a vector. If x is a vector, t a member of G and u a real number, then $x(t)$ will denote the value at t of the linear functional associated with x and $x[u]$ will denote the member of G assigned to u by the one-parameter subgroup associated with x. We convert the set of vectors into a real vector space by carrying over the obvious vector space operations in the set of linear functionals. We note that $(x_1 + x_2)[u] = x_1[u]x_2[u]$ and $u_1x[u] = x[u_1u]$ whenever x, x_1 and x_2 are vectors and u, u_1 and u_2 are real numbers. The natural question concerning the existence of vectors is answered by the

THEOREM. *Let G be a locally compact Abelian group and let G be its character group. Then the following statements about G and $\hat{G}$ are equivalent.*

(*a*) For each t in G distinct from the identity e there exists a linear functional x with $x(t) \neq 0$.

(*b*) For each t in G distinct from e there exists a real character r with $r(t) \neq 1$.

(*c*) The union of the images of all one-parameter subgroups of $\hat{G}$ is dense in $\hat{G}$.

(*d*) $\hat{G}$ is connected.

(*e*) G is the direct product of a discrete torsion free group and the additive group of an n dimensional vector space.

The Laplace Transform.—We define the generalized Laplace transform by replacing the ordinary characters of the Fourier transform theory by the generalized characters described above. The Laplace transform of a suitably restricted function[2] f defined on G is then $\int f(t)(t, z)dt$ where (t, z) is the value at t of the generalized character z. In view of the remarks of the preceding section we may write this as $\int f(t) \exp(x(t))(t, y)dt$ where y is an ordinary character and x is a vector. The result may be regarded as a function defined in the direct product of the space $\bar{G}$ of all vectors with $\hat{G}$. If G is taken to be the additive group of integers then $\hat{G}$ is the multiplicative group of complex numbers of modulus one and $\bar{G}$ may be put in to one-to-one correspondence with the positive real numbers in such a way that the positive real number r corresponds to the linear functional which carries n into $n \log(r)$ and hence to the real character which carries n into r^n. Thus the Laplace transform in this case may be regarded as mapping doubly infinite sequences $\{a_n\}$, $n = \pm 1, \pm 2, \ldots$, into functions defined in the complex plane with the origin removed. It is readily seen to coincide with the corresponding mapping defined by the Laurent series. If G is taken to be the additive group of real numbers, $\bar{G} \times \hat{G}$ turns out to be isomorphic to the additive group of all complex numbers and the transform considered here reduces to the classical doubly infinite Laplace transform. Taking finite direct products of these groups with themselves we obtain multiple Laplace transforms and Laurent series in several complex variables. It follows from the theorem of the preceding section that there is little if any point in considering groups for which G is not connected. With this in mind we may say that roughly speaking the generalized Laplace transform defined above is the "direct product" of the classical n-fold doubly infinite Laplace transform and a transform which generalizes a multiple Laurent series to the same extent that a general discrete torsion free group generalizes a direct product of finitely many replicas of the additive group of the integers.

There are many questions that may be asked about the nature of the subset of $\bar{G} \times \hat{G}$ in which $\int f(t) \exp(x(t))(t, y)dt$ is defined. The answers to these depend, of course, upon the sense in which the integral is to exist. We shall remark here only that if the integral is required to be absolutely convergent then the region of existence is the direct product of a convex subset of $\bar{G}$ with the whole of $\hat{G}$. This, of course, implies at once the well-known facts about the regions of absolute convergence of Laurent series and doubly infinite Laplace transforms.

Analyticity of the Laplace Transform.—Partial differentiation of functions defined on a topological group may be defined by means of one-parameter subgroups. If f is a function defined on $\hat{G}$ and x is any member of $\bar{G}$ the

partial derivative f_x of f with respect to x may be defined as the limit as u tends to zero of $(1/u)(f(yx[u]) - f(y))$ provided that this limit exists in some appropriate sense. If f is the Fourier transform of a suitably restricted function k on G then f_x will be the Fourier transform of the function g on G such that $g(t) = x(t)k(t)$ for all t in G.

Since G is a real vector space it is clear that when it is provided with any reasonable topology there will be a natural one-to-one correspondence between its elements and its one-parameter subgroups and, accordingly, such a correspondence between the elements of $\bar{G} \times \bar{G}$ and the one-parameter subgroups of $\bar{G} \times \hat{G}$. Thus if (x_1, x_2) is a member of $\bar{G} \times \bar{G}$ and F a suitably restricted function defined in $\bar{G} \times \hat{G}$ we may speak of the partial derivative $F_{(x_1, x_2)}$ of F with respect to (x_1, x_2). It is clear that if u is any real number then the partial derivative of F with respect to $u(x_1, x_2) = (ux_1, ux_2)$ is equal to the product of u and the partial derivative of F with respect to (x_1, x_2). Now $\bar{G} \times \bar{G}$ may be converted into a complex vector space by defining $(u + iv)(x_1, x_2)$ to be the element $(ux_1 - vx_2, vx_1 + ux_2)$ but it will, of course, not always be true that the above homogeneity relationship will continue to hold for complex multipliers. Given any class of differentiable functions those members F for which $F_{(x_1, x_2)}$ is a complex homogeneous[3] function of (x_1, x_2) will be referred to as the analytic functions in that class.

As is to be expected there are theorems connecting the properties of being analytic and of being a Laplace transform. We shall close this section by describing such a theorem. Let f be any function in L^2 on G. Then, as may be proved without difficulty, the set of all x in $\bar{G}$ for which $f(t) \exp(x(t))$ is in L^2 on G is a convex subset K_f of $\bar{G}$ and contains the zero element. We shall call a convex subset of $\bar{G}$ large if it contains the zero element and the smallest linear subspace of $\bar{G}$ containing it is the whole of $\bar{G}$. We shall call a point x in a large convex subset of $\bar{G}$ an interior point if, for some real number u greater than one, the point ux is also in the convex subset. A function f for which K_f is large will be said to be strongly in L^2. If f is strongly in L^2 then the function on $K_f \times \hat{G}$ which for each x in K_f is defined for almost all y in $\hat{G}$ as the Fourier transform of $f(t)\exp(x(t))$ we shall call the L^2 Laplace transform of f. Now let K be any large convex subset of $\bar{G}$ and let F be a function defined on $K \times \hat{G}$ so as to be in L^2 on $\hat{G}$ for each x in K. Then for each x in the interior of K the expression $(1/u)(F(x + ux_1, yx_2[u]) - F(x, y))$ may for each (x_1, x_2) be regarded as a one-parameter family of elements of L^2 on $\hat{G}$ defined for u sufficiently small. If this family tends to a limit as u approaches zero for all x interior to K and all (x_1, x_2) in $\bar{G} \times \bar{G}$ and if this limit $F_{(x_1, x_2)}$ is complex homogeneous as a function of (x_1, x_2) we shall say that F is L^2 analytic interior to $K \times \hat{G}$. These definitions having been made, our theorem may be stated as follows.

THEOREM. *Let F be defined on $K \times \hat{G}$ where K is a large convex subset of $\bar{G}$. Then F is L^2 analytic interior to $K \times \hat{G}$ if and only if there exists a function f strongly in L^2 on G such that K_f contains the interior of K and F coincides[4] interior to $K \times \hat{G}$ with the L^2 Laplace transform of f. If f does exist it is unique (modulo functions zero almost everywhere) and $F_{(x_1, x_2)}$ is also analytic and is the L^2 Laplace transform of the function g such that $g(t) = f(t)(x_1(t) + ix_2(t))$.*

Complex Integration and the Cauchy Formula.—If F is the Laplace transform of a function f on G then for each x in $\bar{G}$ it is the Fourier transform of $f(t) \exp(x(t))$. Thus (formally) $\int (F(x, y)/(t, y))dy = f(t) \exp(x(t))$ so that $\int (F(x, y)/(\exp(x(t))(t, y)))dy = f(t)$. In other words, for suitably restricted functions, f may be recovered from F by integrating $F(x, y)/(\exp(x(t))(t, y))$ over any subset of $\bar{G} \times \hat{G}$ which lies in the region of definition of F and is of the form $x_0 \times \hat{G}$; the measure being the Haar measure in $\hat{G}$ transferred by the one-to-one mapping $y \to x_0, y$. It follows that F is determined by its values on any subset of the form $x_0 \times \hat{G}$ and we are led to expect a formula giving $F(x, y)$ in terms of $F(x_0, y)$. If we follow through the formal work of finding f from $F(x_0, y)$ and $F(x, y)$ from f and replacing the Fourier transform of a product by the convolution of the Fourier transforms we get the formula $F(x, y) = \int F(x_0, y_1)K(x - x_0, yy_1^{-1})dy_1$ where $K(x, y)$ is the Fourier transform of $\exp(x(t))$. Unfortunately, this formalism cannot be made to lead to a theorem since the Fourier transform of $\exp(x(t))$ does not exist. Suppose, however, that ϕ is the characteristic function of a set so small that $\phi(t) \exp(x(t))$ does have a Fourier transform for all x in a suitably large subset of $\bar{G}$. Then if f vanishes outside of this set so that $f = \phi f$ the procedure described above leads to the formula $F(x, y) = \int F(x_0, y_1)K_\phi(x - x_0, yy_1^{-1})dy_1$ where $K_\phi(x, y)$ is the Fourier transform of $\phi(t) \exp(x(t))$. This formula may be proved rigorously for suitably restricted functions F. In the case in which G is the additive group of the integers and ϕ is the characteristic function of the non-negative integers it reduces to the classical Cauchy integral formula for the special case in which the closed curve is a circle with center at the origin.

If $\bar{G}$ is finite dimensional (and probably with even a weaker restriction) it is possible to extend the above considerations to the case in which the integration is performed over a much more general subset of $\bar{G} \times \hat{G}$ than one of the form $x_0 \times \hat{G}$. Let ψ be a suitably differentiable function defined throughout $\hat{G}$ and having values in $\bar{G}$. Let C_ψ be the set of all points of $\bar{G} \times \hat{G}$ of the form $\psi(y), y$ for $y \in \hat{G}$. Then a complex valued measure μ_ψ may be introduced into C_ψ which is of such a nature that theorems can be proved establishing the formulae:

$$f(t) = \int_{C_\psi} (F(x, y)/(\exp(x(t))(t, y)))d\mu_\psi$$

and

$$F(x, y) = \int_{C_\psi} F(x_1, y_1)K(x - x_1, yy_1^{-1})d\mu_\psi$$

where, in the second integration, x and y are regarded as fixed. As the work necessary to remove obviously too restrictive conditions from the statements of such theorems has not yet been done we shall confine ourselves here to a description of the measure μ_ψ. Let θ be the function taking y in $\hat{G}$ into $\psi(y)$, y in $\bar{G} \times \hat{G}$. Then θ is a one-to-one map of $\hat{G}$ onto C_ψ and hence μ_ψ is completely determined by the measure in G defined by the equation $\tilde{\mu}_\psi(E) = \mu_\psi(\theta(E))$. When ψ is sufficiently differentiable $\tilde{\mu}_\psi$ will be absolutely continuous with respect to the Haar measure in G and hence will be completely described by its Radon Nikodym derivative with respect to this Haar measure. This derivative may be computed from ψ as follows. For each x in $\bar{G}$ the partial derivative ψ_x of ψ with respect to x may be defined in a manner strictly analogous to that used for complex valued functions. The result will be linear in x and will be for each y in $\hat{G}$ a member of $\bar{G}$. Thus for each y in $\hat{G}$, $\psi_x(y)$ defines a linear transformation $T_\psi(y)$ of the vector space $\bar{G}$ into itself. It may be extended to a complex linear transformation of $\bar{G} \times \bar{G}$ into itself in a unique and obvious fashion. The sought for Radon Nikodym derivative r is defined by the equation: $r(y) = (1/i^n)$ determinant $(iI + T_\psi(y))$. Here I represents the identity transformation and n is the dimension of $\bar{G}$. Presumably a measure with similar properties may be introduced into C_ψ when ψ is only assumed to have some property analogous to being of bounded variation. How this is to be done is a matter which we expect to investigate.

Concluding Remarks.—Among other results in our possession at the moment is a generalization to functions on $\bar{G} \times \hat{G}$ of Hadamard's three circles theorem. Its proof may be carried out using the same device used by Zygmund and Tamarkin[6] in proving Thorin's generalization of the M. Riesz convexity theorem. This is not surprising once one has observed that Thorin's theorem is essentially the Hadamard three circles theorem for functions of n complex variables. We have also investigated the extension to groups of the Hilbert transform and have used this extension to obtain formulae giving $F(x, y)$ in terms of its values on a set of the form $x_0 \times \hat{G}$ which are different from those discussed in the preceding section. These and other matters we intend to discuss in full in the more detailed paper promised in the introduction.

[1] Weil, A., "L'intégration dans les groupes topologiques et ses applications," *Actualités Scientifiques et Industrielles*, No. 869, Paris, 1940.

[2] Functions mentioned in this note are complex valued except when the contrary is explicitly assumed.

[3] This particular way of formulating analyticity was suggested to the author by the treatment of complex manifolds in an unpublished manuscript of C. Chevalley.

[4] Coincidence here means, of course, having the same value for almost all y for each x.

[5] Cf. Bochner, S., "Group Invariance of Cauchy's Formula in Several Variables," *Ann. Math.*, **45**, 686 (1944).

[6] Tamarkin, J. D., and Zygmund A., "Proof of a Theorem of Thorin, *Bull. Am. Math. Soc.*, **50**, 279 (1944).

ON THE ASYMPTOTIC DISTRIBUTION OF THE SUM OF A RANDOM NUMBER OF RANDOM VARIABLES

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We shall state without proof some results on the asymptotic distribution as $\lambda \to \infty$ of the sum

$$Y = X_1 + \ldots + X_N$$

of a random number of independent random variables, where the X_j have the same fixed distribution function $F(x) = P[X_j \leqslant x]$ and where N is a non-negative integer-valued random variable independent of the X_j, whose distribution function depends on a parameter λ. We shall use the notation

$$a = E(X_j), \quad c^2 = Var(X_j)(0 < c^2 < \infty),$$
$$\alpha = E(N), \quad \gamma^2 = Var(N)(0 \leqslant \gamma^2 < \infty), \quad M = (N - \alpha)/\gamma,$$
$$\theta(t) = E(e^{itM}), \quad \sigma^2 = \alpha c^2 + \gamma^2 a^2, \quad \delta = (\gamma a)/\sigma,$$
$$Z = (Y - E(Y))/\sqrt{Var(Y)} = (Y - \alpha a)/\sigma, \quad \varphi(t) = E(e^{itZ}).$$

THEOREM 1. *If as* $\lambda \to \infty$

$$\sigma^2 \to \infty, \quad \gamma = o(\sigma^2), \tag{1}$$

then for any t, *as* $\lambda \to \infty$

$$\varphi(t) = \theta(\delta t)e^{-1/2t^2(1-\delta^2)} + o(1). \tag{2}$$

COROLLARY 1. *If (1) holds and if as* $\lambda \to \infty$

$$a^2\gamma^2 = o(\alpha), \tag{3}$$

then for any t,

$$\lim_{\lambda \to \infty} \varphi(t) = e^{-1/2t^2}, \tag{4}$$

so that Y *is asymptotically normal.*

COROLLARY 2. *If (1) holds and if* M *has a non-normal limiting distribution function* $G(x)$, *so that*

$$\lim_{\lambda \to \infty} \theta(t) = g(t) \not\equiv e^{-1/2t^2}, \tag{5}$$

and if

$$\lim_{\lambda \to \infty} \frac{\alpha c^2}{\gamma^2 a^2} = s (0 \leqslant s < \infty), \tag{6}$$

then

$$\lim_{\lambda \to \infty} \varphi(t) = g\left(\frac{t}{\sqrt{1+s}}\right) \cdot e^{-\frac{1}{2}t^2(s/1+s)} \tag{7}$$

so that Z has a non-normal limiting distribution function.

It is easy to show that if M has a limiting distribution function $G(x)$ such that $G(x) > 0$ for every x, then as $\lambda \to \infty$, $\alpha \to \infty$ and $\gamma = o(\alpha)$, so that (1) holds.

COROLLARY 3. *If N is asymptotically normal then Y is asymptotically normal.*

An example in which (1) does not hold is the following: for any positive integer λ let N have the values λ, 2λ with $P[N = \lambda] = P[N = 2\lambda] = 1/2$, and let $a = 0$. Then $\sigma^2 = (3\lambda c^2)/2$, $\gamma = \lambda/2$, $\gamma \neq o(\sigma^2)$. Here we may show directly that

$$\lim_{\lambda \to \infty} \varphi(t) = \tfrac{1}{2}\left\{e^{-\frac{1}{2}t^2} + e^{-\frac{3}{2}t^2}\right\},$$

which is the characteristic function of a mixture of two different normal distributions. This is a special case of the following theorem.

THEOREM 2. *If*

$$a = 0, \qquad \lim_{\lambda \to \infty} \gamma/\alpha = r (0 < r < \infty), \tag{8}$$

and if M has a limiting distribution function G(x) (necessarily such that G(x) = 0 for some x), then

$$\lim_{\lambda \to \infty} \varphi(t) = \int_0^\infty e^{-\frac{1}{2}t^2 x} dG_1(x), \tag{9}$$

where

$$G_1(x) = G\left(\frac{x-1}{r}\right). \tag{10}$$

It follows that Z has the limiting distribution function

$$H(x) = \int_0^\infty H_0\left(\frac{x}{\sqrt{y}}\right) dG_1(y), \tag{11}$$

where

$$H_0(x) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{x} e^{-\frac{1}{2}u^2} du \tag{12}$$

is the normal distribution function with means 0 and variance 1.

A full account of these results will be published elsewhere.

ON VARIATION-DIMINISHING INTEGRAL OPERATORS OF THE CONVOLUTION TYPE

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A real matrix $A = ||a_{ik}||$, $(i = 1, \ldots, n;\ k = 1, \ldots, m)$, is said to be *totally positive* if all its minors, of any order, are non-negative. The algebraic properties of totally positive matrices have been intensively studied by F. Gantmakher and M. Krein in 1937.[1] In 1930 the author[2] showed that if A is totally positive, then the linear transformation,

$$y_i = \sum_{k=1}^{m} a_{ik}x_k \ (i = 1, \ldots, n), \tag{1}$$

is *variation-diminishing* in the sense that if $v(x_k)$ denotes the number of variations of sign in the sequence $\{x_k\}$ and $v(y_i)$ the corresponding number in the sequence $\{y_i\}$, then we always have the inequality

$$v(y_i) \leqq v(x_k). \tag{2}$$

In a previous note[3] the author has defined the class P of the so-called *Polya frequency functions* as the class of functions $\Lambda(x)$, $-\infty < x < \infty$, satisfying the following three characteristic conditions:

1. $\Lambda(x)$ is measurable.
2. If $x_1 < x_2 < \ldots < x_n$ and $t_1 < t_2 < \ldots < t_n$, then the determinant of order n, whose element in the ith row and jth column is $\Lambda(x_i - t_j)$, should be non-negative, i.e.,

$$\det||\Lambda(x_i - t_j)|| \geqq 0. \tag{3}$$

This inequality should be verified for $n = 1, 2, 3, \ldots$.

3. Finally

$$0 < \int_{-\infty}^{\infty} \Lambda(x)dx < +\infty.$$

All Polya frequency functions $\Lambda(x)$ turn out to be everywhere continuous with the single exception of the so-called truncated exponential

$$\Lambda(x) = \begin{cases} e^{-x} & \text{if } x \geqq 0 \\ 0 & \text{if } x < 0, \end{cases}$$

and all functions arising from it by a change of scale and origin. As stated in the same note, a function $\Lambda(x)$ is equivalent (or equal almost everywhere)

to a Polya frequency function if and only if it has a bilateral Laplace transform of the form

$$\int_{-\infty}^{\infty} e^{-sx}\Lambda(x)dx = \frac{1}{\Psi(s)}, \quad (-a < Rs < a, \text{ for some } a > 0), \tag{4}$$

where $\Psi(s)$ is an entire function of the type II of Laguerre, Polya and Schur[4]

$$\Psi(s) = Ce^{-\gamma s^2+\delta s} \prod_{\nu=1}^{\infty} (1 + \delta_\nu s)e^{-\delta_\nu s}, \tag{4'}$$

(where $C > 0$, $\gamma \geqq 0$, δ, δ_ν real, $0 < \gamma^2 + \Sigma\delta_\nu^2 < \infty$), the relation (4) holding in a certain open vertical strip of the s-plane containing the imaginary axis. Accordingly

$$\Lambda(x) = e^{-x^2}, e^{-|x|}, e^{x-e^x}, 1/\cosh x,$$

are a few examples of Polya frequency functions because their bilateral Laplace transforms are readily found to be of the form (4), (4').

The analogy between the property (3) of a Polya frequency function and the definition of a totally positive matrix A, as given in the first paragraph, would suggest that the convolution transformation,

$$g(x) = \int_{-\infty}^{\infty}\Lambda(x - t)f(t)dt, \tag{5}$$

should be variation-diminishing, provided $\Lambda(x)\epsilon P$. For this purpose we require the following two definitions.

I. Let $f(x)$ be a real function defined for all real x. The number $v(f)$, of variations of sign of $f(x)$ in the range $(-\infty, \infty)$, is defined as follows: If $S: x_1 < x_2 < \ldots < x_n$ is an arbitrary finite increasing sequence of real numbers, then

$$v(f) = \sup_S v(f(x_i)), \qquad (0 \leqq v(f) \leqq \infty).$$

II. Let $\Lambda(x)$ be real and measurable for all real x. We say that the transformation (5) is variation-diminishing if and only if $\Lambda(x)$ enjoys the following two properties:

1.

$$0 < \int_{-\infty}^{\infty} |\Lambda(x)|dx < \infty.$$

2. If $f(t)$ is bounded and measurable, then (5) should always imply the inequality

$$v(g) \leqq v(f). \tag{6}$$

The following theorem holds.

THEOREM. *The convolution transformation*

$$g(x) = \int_{-\infty}^{\infty} \Lambda(x-t)f(t)dt \tag{5}$$

is variation-diminishing if and only if the function $\Lambda(x)$ *admits of a bilateral Laplace transform of the form*

$$\int_{-\infty}^{\infty} e^{-sx}\Lambda(x)dx = \frac{\epsilon}{\Psi(s)} \tag{7}$$

where $\epsilon = \pm 1$ *and* $\Psi(s)$ *is an entire function of the Laguerre-Polya-Schur type (4'), the relation (7) being valid in a certain open vertical strip of the s-plane containing the imaginary axis. An equivalent formulation is as follows: (5) is variation-diminishing if and only if* $\epsilon\Lambda(x)$ *(*$\epsilon = +1$ *or else* $= -1$*) is almost everywhere equal to a Polya frequency function.*

If (5) is variation-diminishing, we always have $v(g) \leqq v(f)$*, even if* $f(t)$ *is not bounded, provided* $f(t)$ *is summable in every finite range and such that the improper integral (5) converges for every value of x. In particular, this is always the case if* $f(t)$ *is a polynomial.*

The variation-diminishing property of the classical transformation,

$$g(x) = \frac{1}{\sqrt{\pi}} \int_{-\infty}^{\infty} e^{-(x-t)^2} f(t)dt,$$

has previously been established by Polya[5] in connection with related work of Laguerre.

In the case of the "rectangular" frequency function

$$\Lambda(x) = \begin{cases} 1/(2h) \text{ if } -h \leqq x \leqq h \\ 0 \text{ if } x > h, \text{ or } x < -h, \end{cases} \tag{8}$$

(5) turns into the familiar "integral-mean" transformation

$$g(x) = \frac{1}{2h} \int_{x-h}^{x+h} f(t)dt \tag{9}$$

which is often used for practical or theoretical smoothing purposes, a fact which may justify the following remarks. The transformation (9) is *not* variation-diminishing, because (8) is not a Polya frequency function. Indeed, the transform of (8) is

$$\frac{1}{2h} \int_{-h}^{h} e^{-sx}dx = \frac{\sinh(sh)}{sh}$$

which is certainly not of the necessary form (7) because it has (infinitely many) zeros. An example when (9) increases the number $v(f)$ is easily constructed as follows. Let n be an integer, $n \geqq 3$, and let

$$f(x) = \begin{cases} 1 + \cos x & \text{if } x < -\pi \text{ or } x > \pi, \\ 1 + \cos x - (n + 1/2) & \text{if } -\pi \leqq x \leqq \pi. \end{cases}$$

Evidently $v(f) = 2$. However, with $2h = (2n + 1)\pi$, we find that (9) transforms our $f(x)$ into $g(x)$, where

$$g(x) = \frac{(-1)}{h} \cos x \text{ in the range } -(n - 1/2)\pi \leqq x \leqq (n - 1/2)\pi.$$

Thus $v(g) \geqq 2(n - 1) > v(f)$.

The term "Polya frequency functions" for the functions of our class P seems justified for the following reasons. Let

$$\frac{1}{\Psi(s)} = \sum_{\nu=0}^{\infty} \frac{(-1)^\nu}{\nu!} \mu_\nu s^\nu, \qquad (\mu_0 \neq 0), \tag{10}$$

be the power series expansion of the meromorphic function (4). Evidently

$$\mu_\nu = \int_{-\infty}^{\infty} \Lambda(x) x^\nu dx, \qquad (\nu = 0, 1, 2, \ldots). \tag{11}$$

If $f(t)$, of (5), is a polynomial of degree n, then (5) may be evaluated as follows:

$$g(x) = \int_{-\infty}^{\infty} \Lambda(t) f(x - t) dt = \int_{-\infty}^{\infty} \Lambda(t) \sum_{\nu=0}^{n} \frac{(-1)^\nu t^\nu}{\nu!} f^{(\nu)}(x) dt$$

or

$$g(x) = \mu_0 f(x) - \frac{1}{1!} \mu_1 f'(x) + \ldots \pm \frac{1}{n!} \mu_n f^{(n)}(x) = \frac{1}{\Psi(D)} f(x).^6 \tag{12}$$

In this connection Polya proved in 1915 the following remarkable result[7]: "Let (10) be a formal power series (*formal* means that no convergence is assumed) with the following property (S): If $f(x)$ is an arbitrary real polynomial, then the number of real zeros of the transformed polynomial $g(x)$, given by (12), should never exceed the number of real zeros of the given polynomial $f(x)$. A power series (10) enjoys the property (S) if and only if it is the Taylor expansion of the reciprocal $\pm 1/\Psi(s)$ of an entire function $\Psi(s)$ of the form (4')." Thus our Theorem was discovered by Polya in 1915 for the case when $f(x)$ and $g(x)$ are polynomials,[8] the convolution transformation (5) being replaced by the differential operator relation (12). These remarks show that the Polya frequency functions $\Lambda(x)$ appear implicitly in Polya's work of 1915 in terms of their moments (11).

In concluding we wish to mention a result of Th. Motzkin which is used in the proof of our Theorem. In 1930 the author showed that the linear transformation (1) is certainly variation-diminishing if the matrix A does not possess two minors of equal orders and of opposite signs. He also showed that conversely, if (1) is variation-diminishing, then A cannot have two minors of equal orders and of opposite signs, *provided the rank of* A *is* $= m$. The necessary and sufficient conditions in order that (1) be variation-diminishing were discovered in 1933 by Th. Motzkin.[9] They

are as follows: Let r be the rank of A; then A should not have two minors of equal orders and of opposite signs if their common order is $<r$, while if their common order is $=r$ then again they should never be of opposite signs if they belong to the same combination of r columns of A.

In his contribution to the Courant Anniversary Volume[10] the author has recently discussed the discrete analog of the problem of the present note, namely, the variation-diminishing (sequence) convolution transformations

$$y_n = \sum_{\nu=-\infty}^{\infty} L_{n-\nu} x_\nu, \qquad (n = \ldots, -1, 0, 1, \ldots); \tag{13}$$

in their relation to the sequences $\{L_n\}$ satisfying the following two conditions: (1) The 4-way infinite matrix $||L_{n-\nu}||$ has only non-negative minors; (2) $0 < \sum_{-\infty}^{\infty} L_\nu < \infty$. These sequences are the discrete analogs of the Polya frequency functions.

[1] Gantmakher, F., and Krein, M., "Sur les matrices complètement non négatives et oscillatoires," *Compositio Math.*, **4**, 445–476 (1937).

[2] Schoenberg, I. J., "Über variationsvermindernde lineare Transformationen," *Math. Z.*, **32**, 321–328 (1930).

[3] Schoenberg, I. J., "On Totally Positive Functions, Laplace Integrals and Entire Functions of the Laguerre-Polya-Schur Type," PROC. NAT. ACAD. SCI., **33**, 11–17 (1947).

[4] Polya, G., and Schur, I., "Über zwei Arten von Faktorenfolgen in der Theorie der algebraischen Gleichungen," *J. Math.*, **144**, 89–113 (1914).

[5] Polya, G., "Qualitatives über Wärmeausgleich," *Z. angew. Math. u. Mech.*, **13**, 125–128 (1933); and also Polya, G., "Sur un théorème de Laguerre," *Compt. rend.*, **156**, 996–999 (1913).

[6] In the present case when $f(x)$, and therefore also $g(x)$, is a polynomial, we may invert the relation (12) by means of the relation $f(x) = \Psi(D)g(x)$. Thus we obtain the inversion of the convolution transformation (5) by the relation $f(x) = \Psi(D)g(x)$, provided $\Lambda(x)$ is a Polya frequency function. Polya frequency functions play an important rôle also in Widder's recent work; indeed, he shows that if $\Lambda(x)$ is a Polya frequency function then (5) is again inverted by $f(x) = \Psi(D)f(x)$, provided $f(x)$ is merely assumed to be continuous and absolutely integrable in $(-\infty, \infty)$ and the relation $f(x) = \Psi(D)f(x)$ is suitably interpreted. See Widder, D. V., "The Inversion of a Generalized Laplace Transform," PROC. NAT. ACAD. SCI., **33**, 295–297 (1947).

[7] Polya, G., "Algebraische Untersuchungen über ganze Funktionen vom Geschlechte Null und Eins," *J. Math.*, **145**, 224–249 (1915), especially page 231.

[8] Polya's statement in terms of the numbers of *real zeros* of the polynomials $f(x)$ and $g(x)$ is really equivalent to our statement in terms of the numbers of *variations of sign* of these functions, as we may easily show the equivalence of these two statements as far as polynomials are concerned.

[9] Motzkin, Th., *Beiträge zur Theorie der linearen Ungleichungen*, (Doctoral dissertation, Basel 1933), Jerusalem, 1936, 69 pp., especially Chap. IV.

[10] Schoenberg, I. J., "Some Analytical Aspects of the Problem of Smoothing," *Courant Anniversary Volume*, New York, 1948, 351–370, especially §2. On page 362 (*loc. cit.*) the transformation (13) is said to be variation-diminishing if: (1) $L_n \to 0$ exponentially

if $n \to +\infty$; (2) for every bounded sequence $\{x_n\}$, (13) implies the inequality $v(y) \leqq v(x)$. The first condition is unnecessarily restrictive; indeed, it is readily seen that Theorem 2 (*loc. cit.*, page 363) and its proof remain valid if we define a variation-diminishing transformation (13) by the following two conditions: (1') $0 < \Sigma|L_n| < \infty$, $L_n > 0$ for some n; (2') $v(y) \leqq v(x)$ for bounded $\{x_n\}$.

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*PHYSICAL CURVES IN GENERALIZED FIELDS OF FORCE**

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1. The differential geometry of the dynamical trajectories and certain important physical systems of curves of general positional fields of force has been developed by Kasner in his Princeton Colloquium Lectures.[1] Recently we have introduced the concept of *generalized* fields of force which depend not only on the position of the point but also upon the direction through the point. Positional fields may be described as *isotropic* and generalized fields as *anisotropic*.[2]

If (ϕ, ψ) are the rectangular components of a generalized field of force in the plane, the corresponding equations of motion of a particle are

$$\frac{d^2x}{dt^2} = \phi(x, y, p), \qquad \frac{d^2y}{dt^2} = \psi(x, y, p). \tag{1}$$

The cartesian coördinates of a point are denoted by (x, y), the slope through the point by $p = dy/dx$, and the time by t. We assume that the slope of the force vector is *not* identical with p. For otherwise, the trajectories are all straight lines and the field of force is of no interest. In a generalized field of force, there are ∞^3 trajectories, just as in the positional case.

Upon eliminating the time t from the differential equations (1) of motion of a particle, we find that *the differential equation of third order defining a generalized dynamical family of* ∞^3 *curves is*

$$(\psi - p\phi)\frac{d^3y}{dx^3} = [\psi_x + p(\psi_y - \phi_x) - p^2\phi_y]\frac{d^2y}{dx^2} + [\psi_p - p\phi_p - 3\phi]\left(\frac{d^2y}{dx^2}\right)^2. \tag{2}$$

2. *A system* S_k of curves in a generalized field of force consists of curves along which a constrained motion is possible so that the pressure P is proportional to the normal component N of the force vector. Thus $P = kN$. There are ∞^3 curves in a given system S_k for a fixed k.

The differential equation of third order defining any system S_k is

$$(\psi - p\phi)\frac{d^3y}{dx^3} = [\psi_x + p(\psi_y - \phi_x) - p^2\phi_y]\frac{d^2y}{dx^2} + [\psi_p - p\phi_p - 3\phi - \frac{(n-2)(\phi + p\psi)}{1+p^2}]\left(\frac{d^2y}{dx^2}\right)^2 \quad (3)$$

The relation between k and n is

$$n = \frac{2}{k+1}. \quad (4)$$

The system S_k is undefined for $k = -1$ or $n = \infty$.

The important systems of physical interest are:

The system S_0 of *trajectories* defined by $k = 0$ or $n = 2$.
The system S_1 of *general catenaries* defined by $k = 1$ or $n = 1$.
The system S_{-2} of *general brachistochrones* defined by $k = -2$ or $n = -2$.
The system S_∞ of *velocity curves* defined by $k = \infty$ or $n = 0$.

3. Every system S_k of ∞^3 curves is of *the type* (G), that is, it is defined by a differential equation of third order of the form

$$\frac{d^3y}{dx^3} = G(x, y, p)\frac{d^2y}{dx^2} + H(x, y, p)\left(\frac{d^2y}{dx^2}\right)^2. \quad (5)$$

Conversely we have proved that *except for the velocity systems* S_∞, *any family of* ∞^3 *curves of the type* (G) *always represents a system* S_k *in a generalized field of force. There are* $\infty^{f(2)}$ *such fields of force.*

On the other hand, we have shown that a *family of curves of the type* (G) *is a velocity system* S_∞ *if and only if it is a system of curvature trajectories.*

Thus the differential equation of third order defining any velocity system S_∞ is

$$\frac{d^3y}{dx^3} = (\alpha_x + p\alpha_y)\frac{d^2y}{dx^2} + \alpha_p\left(\frac{d^2y}{dx^2}\right)^2. \quad (6)$$

This system of ∞^3 curves consists of the curvature trajectories of the family of ∞^2 curves: $d^2y/dx^2 = e^{\alpha(x, y, p)}$.

For the positional case, the functions G and H need to be specialized further. A characteristic set of *five geometric properties* for the system S_k in positional fields of force have been obtained by Kasner.[3]

4. We shall define the angular rate λ which is associated with any lineal-element E of the plane for the motion of a particle when acted upon by a generalized field of force. As the lineal-element E rotates about its point P, the corresponding force vector F also rotates about P. The *angular rate* λ is the instantaneous rate of change of the inclination of F with respect to the inclination of E. It is given by the formula

$$\lambda = \frac{(1 + p^2)(\phi\psi_p - \psi\phi_p)}{\phi^2 + \psi^2}. \tag{7}$$

For any ordinary positional field of force, $\lambda = 0$. However, the angular rate λ vanishes not only for positional fields but also for those generalized fields of force such that the direction of the force vector at any point P does not vary but its magnitude does.

The possible *lines of force* are defined by

$$\psi(x, y, p) - p\phi(x, y, p) = 0. \tag{8}$$

Along any line of force, the angular rate λ is

$$\lambda = \frac{\psi_p - p\phi_p}{\phi}. \tag{9}$$

If there exists a lineal-element E_0 which satisfies (8) and if $\lambda \neq 1$ at E_0, then (8) can be solved for p in the neighborhood of E_0, that is, $p = f(x, y)$. In general, this has ∞^1 integral curves, namely, the lines of force.

5. At a point P, there is, in general, a *single particular curve* C_0 of the system S_k such that the particle describing this curve C_0 has zero speed at P. The direction of C_0 at P coincides with that of the force vector. Conversely there are ∞^1 curves of the system S_k in the direction of the force vector. The particle describing each one of these curves except C_0 have speeds different from zero at P; but then the curvatures are zero at P. For the particular curve C_0, the speed of the particle at P is zero but its curvature at P is *not* zero in general. For the system S_0 of trajectories, the curve C_0 is the rest trajectory. In any system S_k, there are ∞^2 such curves C_0.

The ratio ρ of the curvature of the particular curve C_0 to the curvature of the tangent line of force, is

$$\rho = \frac{1 - \lambda}{1 + n - \lambda} = \frac{(1 + k)(1 - \lambda)}{(3 + k) - (1 + k)\lambda}. \tag{10}$$

For the system S_0 of trajectories, this is $\rho = (1 - \lambda)/(3 - \lambda)$.

For the system S_1 of catenaries, this is $\rho = (1 - \lambda)/(2 - \lambda)$.

For the system S_{-2} of brachistochrones, this is $\rho = (\lambda - 1)/(\lambda + 1)$.

For the system S of velocity curves, this is $\rho = 1$.

The above result generalizes various extensions of the theorem of Kasner concerning one-third of the curvatures.[4]

6. *An arbitrary lineal-element transformation, not necessarily of the contact type, will send the ∞^3 curves of every system S_k (including $k = \infty$) into the ∞^3 curves of a system S_k if and only if it is an extended collineation or correlation.*

In the positional case, we have proved that the only transformations

which convert every system S_k except $k = 0$ into a system S_k are the similitudes. The only appropriate transformations for the systems S_0 are the collineations (related to Appell's transformation).

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[1] Kasner, "Differential-Geometric Aspects of Dynamics," *Am. Math. Soc. Colloquium Publ.*, **3**, 1913 (1934). Also see series of papers in *Trans. Am. Math. Soc.*, **7–11**, (1906–1910).

[2] Kasner and De Cicco, "A Generalized Theory of Dynamical Trajectories," *Ibid.*, **54**, 23–38 (1943).

[3] Kasner, "Physical Curves," PROC. NAT. ACAD. SCI., **33**, 246–251 (1947).

[4] De Cicco, "Constrained Motion Upon a Surface Under a Generalized Field of Force," *Bull. Am. Math. Soc.*, **53**, 993–1001 (1947). Kasner and Mittleman, "A General Theorem on the Initial Curvatures of Dynamical Trajectories," PROC. NAT. ACAD. SCI., **28**, 48–52 (1942).